ECOLOGIC PLANT GEOGRAPHY OF THE PACIFIC NORTHWEST

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The purpose of this phytogeographic sketch is to provide an introduction to the natural vegetation of the Pacific Northwest for the use of botanists from other areas who will be attending the XI International Botanical Congress in Seattle in 1969. Attention will be centered on the State of Washington, with secondary emphasis on the adjoining areas. If my friends in British Columbia feel that I have slighted their Province, this is more a consequence of maps terminating at the international border than of any intent of mine to confine attention to the "Pacific Northwest,"—a nationalistic and ambiguous though useful term, which I shall not try to define!

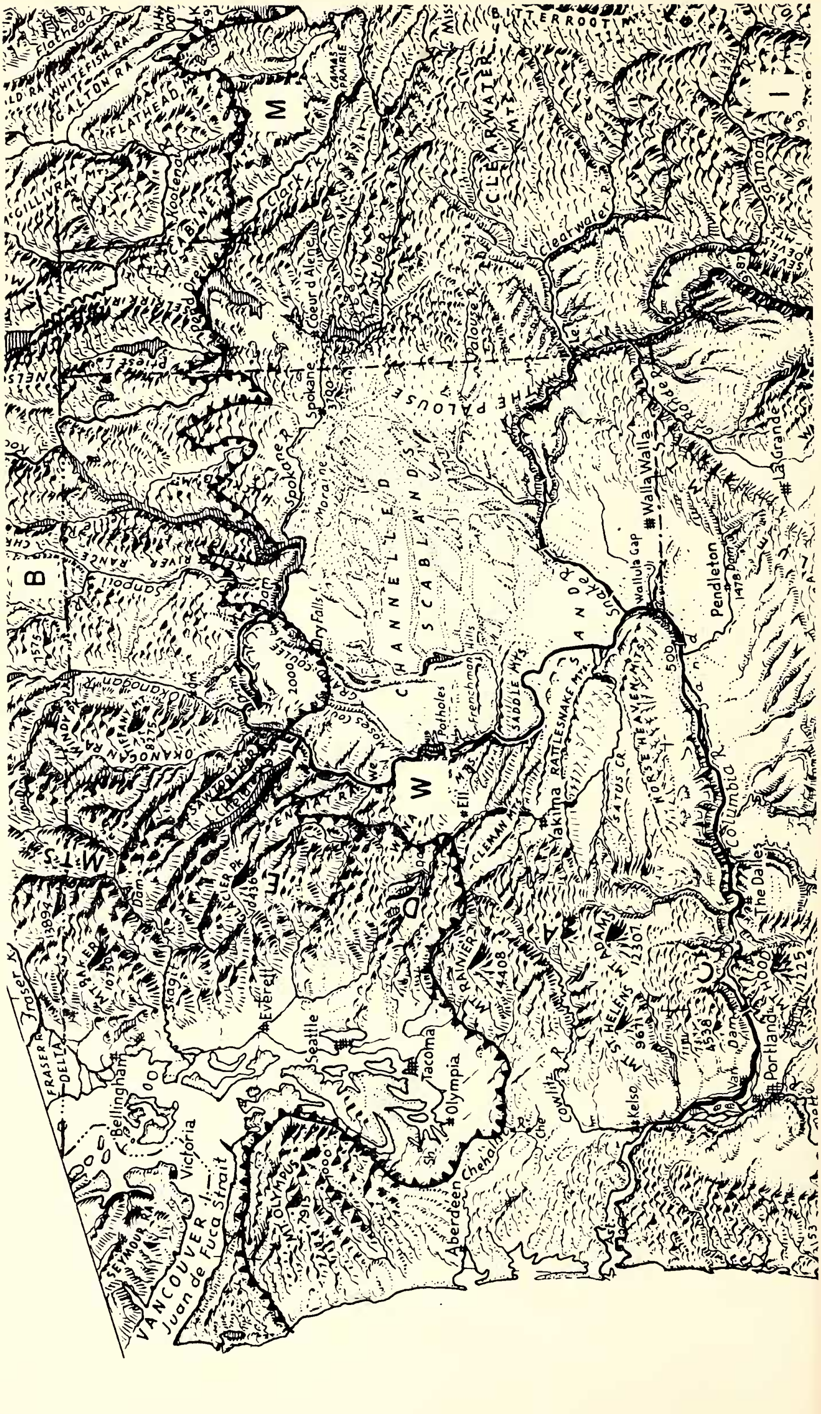
The visitor, like some of us who reside here, may be appalled by the scarcity of natural vegetation in a region which was opened up by white explorers as late as 1805 (the Lewis and Clark expedition). Nevertheless the account is centered on remnants of natural vegetation with the intent of helping the visitor recognize some of the common types and see how they fit into a regional pattern.

The Land Surface

The Rocky Mountains (only a limited fringe of them shows at the right edge and upper half of fig. 1) are the oldest of our major mountain systems, the uplifting and folding that first gave them definition having taken place well back in the Cenozoic Era. Their rocks are partly granitic and partly sedimentary, and show a wide variation in the degree of metamorphism, but neither chemically nor physically do they present extreme conditions that h ave been acclaimed of much phytogeographic importance.

Later in the Cenozoic another major geologic event of interest to us here was the building up of a great basaltic plateau of some 26,000,000 ha^2 in extent that covered the non-mountainous parts of eastern Washington, eastern Oregon, and southern Idaho. Layers of the columnar basalt that comprise this plateau are conspicuous features of canyon walls throughout the plateau region.

In Pliocene time the Cascades were uplifted, these mountains reaching considerable height and thereby stimulating so much rainfall that their basaltic veneer was in large part soon eroded away exposing the intrusive core. Since basalt gives rise to much more fertile soil than acid igneous rocks, there are some significant botanical differences to be observed in going from basaltic to granitic areas. For example, from Mt. Rainier southward basalt is the prevailing rock still mantling the Cascades, whereas northward acid igneous rocks outcrop. The ubiquity of *Purshia*


Flathead
WHITEFISH RA.
GALTON RA.
FLATHEAD
CABINET MTS.
Kootenai
Clark Fk.
CAMAS PRAIRIE
BITTERROOT MTS.
CLEARWATER MTS.
Clearwater R.
Coeur d'Alene
St. Joe R.
Salmon
SEVEN DEVILS MTS.
SELKIRK RA.
Pend Oreille
Priest L.
Palouse R.
THE PALOUSE
Spokane
Spokane R.
3700
Moraine
CHANNELED SCABLANDS
Snake R.
Wallula Gap
Walla Walla
Grande Ronde R.
La Grande
Pendleton
1478
500
RIVER RANGE
Sanpoil
Okanogan R.
Dry Falls
2000
COULEE
Moses Cou.
Potholes
Frenchman Hills
SADDLE MTS.
RATTLESNAKE MTS.
HORSE HEAVEN MTS.
SATUS CR.
Columbia R.
OKANOGAN RA.
WINDY PK.
8275
SAWTOOTH RIDGE
Chelan
ENTIAT RA.
Ell.
CLEMAN MTS.
Yakima
Dam
Pk.
10436
13894
MT. BAKER
10750
Skagit R.
Everett
Seattle
Tacoma
Olympia
MT. RAINIER
14408
MT. ADAMS
12307
MT. ST. HELENS
9671
Cowlitz R.
Kelso
The Dalles
MT. HOOD
11225
Portland
Vancouver
Dam
4538
Fraser R.
FRASER DELTA
Bellingham
Victoria
VANCOUVER I.
Juan de Fuca Strait
SEYMOUR RA.
MT. OLYMPUS
7915
Aberdeen
Chehalis R.
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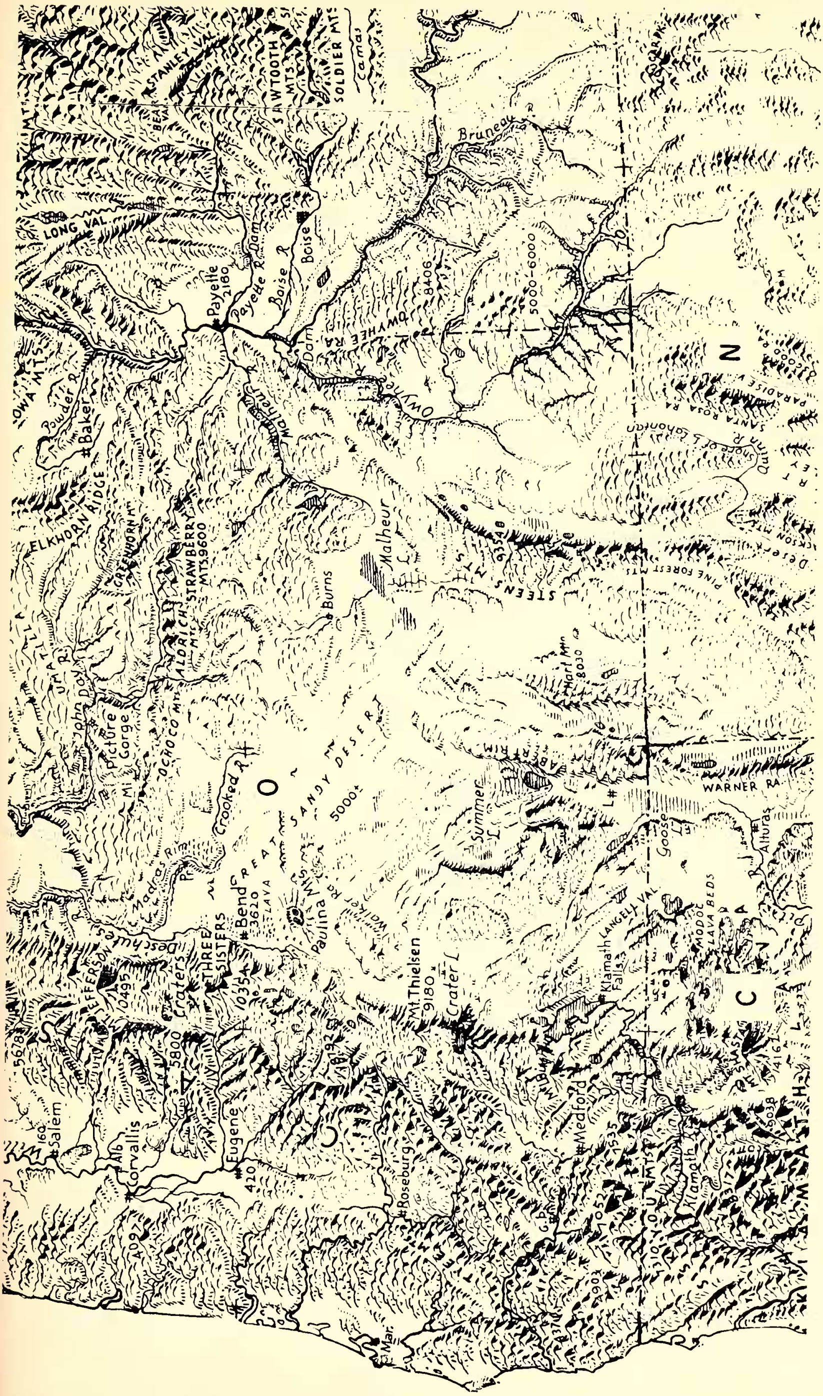
STANLEY VAL.
SAWTOOTH MTS.
SOLDIER MTS.
Camas
Bruneau R.
LONG VAL.
Payette
2180
Payette R.
Boise R.
Boise
OWYHEE RA.
8406
5000-6000
Owyhee R.
Powder R.
Baker
ELKHORN RIDGE
GREENHORN
STRAWBERRY MTS. 9600
Malheur R.
Malheur L.
Burns
STEENS MTS.
9354
SANTA ROSA RA.
PARADISE V.
PINE FOREST MTS.
John Day R.
Picture Gorge
OCHOCO MTS.
Crooked R.
SANDY DESERT
5000±
Hart Mtn
8030
ABERT RIM
WARNER RA.
Summer L.
Goose L.
Alturas
Madras
Bend
3620
LAVA
Paulina Mts.
Walker Ra.
Deschutes
JEFFERSON
10495
Craters
THREE SISTERS
10354
5800
Mt. Thielsen
9180
Crater L.
Klamath Falls
LANGELL VAL.
MODOC LAVA BEDS
14162
Salem
160
Corvallis
Eugene
420
Roseburg
Medford
Klamath R.
WARNER RA.

tridentata in the igneous foothills, in contrast with its restriction to a few special habitats in the basalt area to the south is correlaed with this geologic discontinuity.

In Fig. 1 a chain of low mountains is shown following the Pacific shoreline. These are the Coast Ranges. They are well developed in southwestern Oregon where they merge with the Cascades, but otherwise they are quite low in Oregon and Washington with the outstanding exception of the Olympic Mountains. To the north in British Columbia they again become imposing features of the land.

Continental glaciation terminated in Washington and northern Idaho (fig. 1), leaving the area to the north mantled with glacial till. In places melt waters flowing outward from the ice cut great chasms in the basalt flows, and elsewhere washed the surface clean in broad drinageways, depositing large sheets of gravel and sand farther downstream.

Vulcanism during the late Cenozoic raised a string of spectacular volcanic peaks far above the general level of the Cascade crest from British Columbia to California, but spectacular as these peaks are, their major significance for ecology lies in the ejecta spread over the landscape when two of them erupted.

In approximately 12,000 B.C. Glacier Peak, situated a little to the northwest of the center of Washington in Fig. 1, erupted and winds at that time spread fine white ash over considerable area to its leeward. Then in 6600 B.C. the stupendous explosion of Mt. Mazama, in the southwest quarter of Oregon in Fig. 1, gave rise to a blanket of materials so deep and extensive as to dwarf the Glacier Peak event. (Crater Lake now occupies the vent where Mt. Mazama exploded.) Fine white ash fanned out eastward and northward over most of the Pacific Northwest, extending well into British Columbia and Montana, to provide a valuable marker in sediments that has been generally useful in geochronology, archaeology and the correlation of fossil sequences in bogs. In the more immediate vicinity of Mt. Mazama coarse pumice was deposited to great depths, smothering pre-existing vegetation and providing a substrate that supports highly distinctive vegetation even today. For example, *Pinus contorta,* nearly everywhere a seral tree in the mountains, is the only tree that can grow over a large portion of the pumice area, and here it maintains reproduction as a climax dominant.

In some period prior to the last (Wisconsin) glaciation there were several episodes of loess accumulation on the basaltic plateau between

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FIG. 1. Physiography of Washington and Oregon, with adjoining parts of British Columbia, Idaho, Nevada and California. These state and province names have been indicated only by centrally placed letters, respectively: W, O, BC, I, N and C. The ornamented line crossing the map in the approximate latitude of central Washington indicates the southern limits of the last (Wisconsin) continental glaciation. Areas subjected to mountain glaciation are not indicated. Map reproduced through the courtesy of Edwin Raisz and the publishers of W. W. Atwood's "Physiographic provinces of North America."

the Cascades and the Rockies. The volcanic ash which fell later became incorporated with this loess, or in places was washed into hollows. On the forest-covered mountain slopes the ash was trapped and fixed where it fell, giving the forest of northern Idaho in particular a relatively complete cover of fine-textured fertile material (usually very fine sandy loam) so that the occurrence of thin stony soil is not so important a factor in forest ecology there as in most mountain areas of western North America. Down on the basal plain in Washington, the loess mantle with its incorporated ash was in places stripped away in the path of extensive Wisconsin glacial floods, so that desert-like areas of bare basalt became exposed. These areas which support sparse vegetation mainly of dwarf shrubs and the tiny caespitose grass *Poa secunda,* are labelled "channelled scablands" in Fig. 1.

Other botanically significant geologic features which are more localized are the outcroppings of serpentine (southwestern Oregon and the east slope of the Cascades in central Washington), recent outpourings of lava (locally in the Cascades of Washington and Oregon, and especially in Craters of the Moon National Monument in southern Idaho), and cones of coarse ejecta that dot the landscape in central Oregon, and form Mt. St. Helens in Washington.

Climate

Far greater climatic complexity is encountered in the surroudings of these meetings than has characterized the areas where most of the preceding congresses have convened. All of those areas had diversity resulting from the latitudinal climatic gradient, and some had a significant superimposed gradient, usually extending more or less at right angles, that involved degrees of oceanicity or continentality. But it would be difficult to find a match for the intensification of the north-south climatic gradient that results from the strong influence of the Westerlies that are centered approximately on the Canada-United States border, or a match for the steepness of the oceanic-continental gradient that results from massive mountains rising to height of several thousand meters within a few km of tidewater.

When the topographic map (fig. 1) is compared with the precipitation map (fig. 2), the "approach effect" is clearly shown by the high precipitation on lowlands as the Westerlies approach major mountain masses from the southwest. A sizable area in the lowlands to the southwest of the Olympic Mountains has precipitation in excess of 2,540 mm a year. Quinault Ranger Station has an average annual value of 3,414 mm. It is in this general area that cryptogamic epiphytes are so spectacularly developed, and a trip up the Hoh or Quinault Valleys is eminently worthwhile to see the phenomenon. The approach effect is again evident along the west base of the Cascades and even along the west base of the Rockies across the arid intermountain trough.

The effect of mountains on precipitation also has its negative aspect, the creation of a relatively dry rain shadow along the leeward base of each of the major mountain masses. To the northeast of the Olympic Mountains a weak but well-defined rain shadow provides many more sunny days at places like Sequim than in surrounding areas, with the influence clearly discernible even in Seattle and on the nearby islands in Puget Sound. The most pronounced rainshadow is along the eastern base of the Cascades in central Washington. In the Yakima Valley the mean annual precipitation drops as low as 175 mm within easy sight of heavy forests of mesophytic conifers that encircle the glacier-clad slopes of Mount Rainier where precipitation is at least 2,972 mm. Both the rainshadow and the approach effect are well illustrated (from British Columbia to Oregon) by both weather statistics and the resultant vegetation patterns.

Not only does our precipitation vary greatly from one place to another but its unequal distribution throughout the year is botanically important. Each summer the belt of the Westerlies recedes northward, and failing to drag heavy supplies of moisture inland at this season, the summers are left remarkably short of precipitation. Where the annual sum is low, the shortage becomes critical, and those who visit the rainshadow at the east flank of the Cascades will experience weather that for a few months in summer remind one of true desert conditions. Only the coolness and shortness of summers west of the Cascades (the spring and autumn seasons are quite long) keep drouth from reaching serious proportions there.

Winter rains are gentle and almost mistlike, often accompanied by heavy cloud and fog that bedevil air transportation. Coastal areas get only half the possible hours of sunshine. In summer convectional showers are so rare that storm-induced erosion is not severe. Strangers seeing the wheatlands of southeastern Washington (the "Palouse" in fig. 1) for the first time are usually amazed at the sight of cultivated slopes so steep that self-levelling harvesting machines are used, and the trucks that service them frequently overturn. Such slopes are not cultivatable under rainfall conditions that prevail toward the center of the continent.

Along the coast the frost-free season is approximately 250 days long, and snow is rather ephemeral, whereas in the mountains frost is likely any day in summer and snowbanks may persist throughout the summer even in the subalpine forest belt.

In winter a high pressure system forces Arctic air masses southward down the plain east of the Rockies and often this air spills over the mountains westward to temporarily overwhelm the oceanic character of the climate between the Rockies and the Cascades. These sudden cold spells are very damaging to fruit trees and ornamentals (all aliens), and sometimes even the native plants are damaged. The Columbia Gorge is large enough to allow oceanic influences to penetrate inland readily, and often cold air influences extend farthest west down this gorge. At its western extremity many trees are flag-shaped in consequence of ice storms in winter when cold air pours westward down the valley, and at the eastern extremity they are flag-shaped in the opposite direction by the pressure of winds blowing eastward while branches are actively growing.

Soils

In discussing "the land surface" the general character of the parent materials for soils has been indicated. In Fig. 3 the types of profiles that might be expected on deep loams of undulating topography are shown. These zonal soils are closely related to the pattern of rainfall, but since there are large areas of steep topography in which surface materials are moved by gravity from time to time, the large areas of parent material of geologically recent origin (sand and gravel, bare rock, volcanic ejecta, desiccated lake beds, etc.), the map units are highly complex mixtures of azonal, intrazonal, and zonal soils.

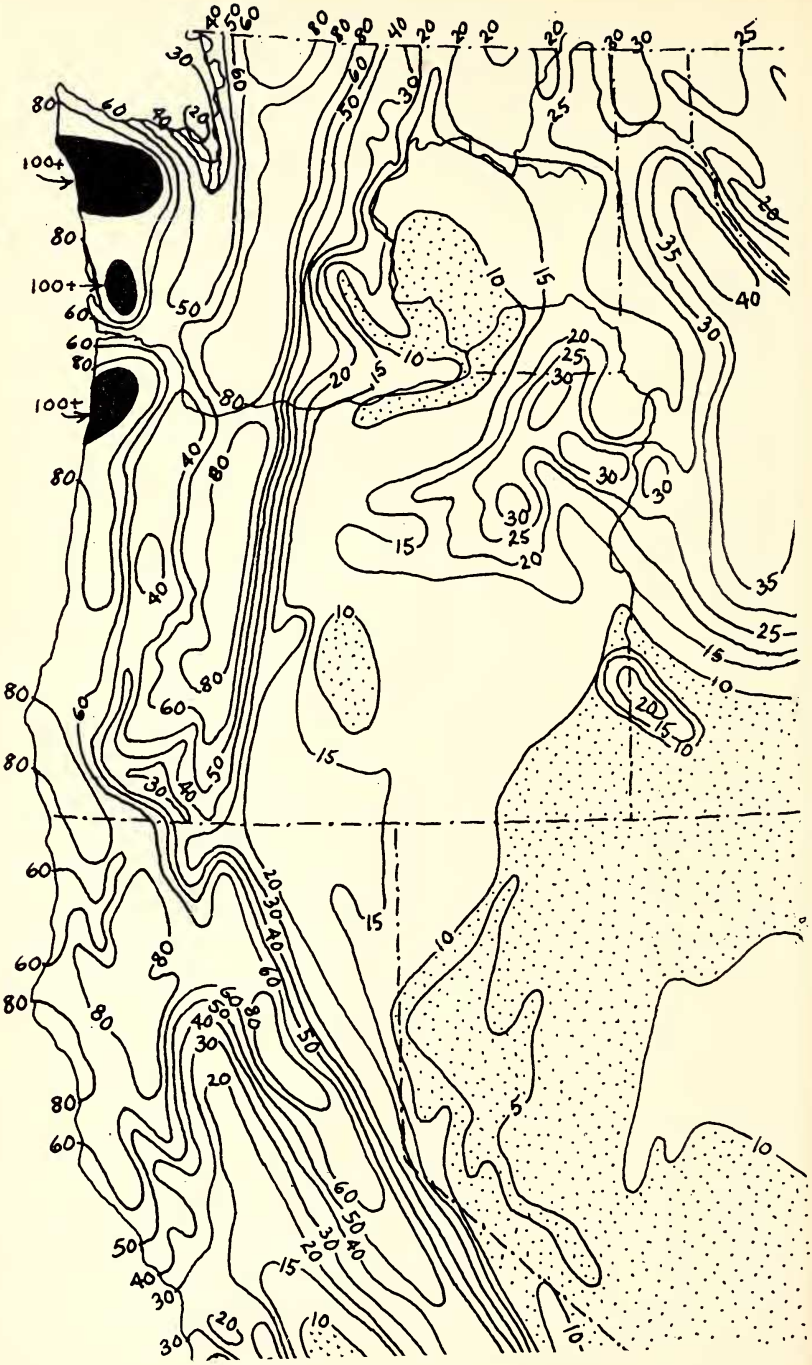
Alpine Vegetation

Where the mountains rise so high that heat is no longer adequate to allow the development of the tree life-form, the vegetation of the treeless area is called alpine tundra (figs. 4, 5). Near the coast the elevation of this ecologically critical level is about 900 m in west central British Columbia, rising to about 2,700 m at the southern end of the Cascade Mountains in California. Eastward in the more continental climates of the Rocky Mountains the critical level is about 800 m higher at equivalent latitudes. Although this timberline is relatively stable, one can frequently see evidence of trees having invaded contiguous areas of herbaceous vegetation, with most of the invasion having taken place during the very dry period in the early 1930's.

In the highest part of the alpine region glaciers and lichen-covered rock debris dominate the landscapes, whereas down next to timberline lush meadows dominated by forbs (*Lupinus, Castilleja, Valeriana, Pedicularis, Anemone*) mixed with graminoids, or by low shrubs (*Empetrum nigrum, Luetkea pectinata, Phyllodoce, Cassiope*) prevail. At intermediate elevations there are stony fell fields where the plant cover is incomplete and cushion plants exemplified by the holarctic *Silene acaulis* are best developed. Mid- to late July is approximately the height of the flowering season for alpine plants in west central North America. The communities they form have been well studied only in Montana.

Subalpine Forests

The forests just below upper timberline differ considerably on either side of a line drawn a little east of the divide of the Cascades (figs. 4, 5). East of this line *Abies lasiocarpa* and *Picea engelmannii* are the conspicuous species in old-growth stands. Since they are geologically recent derivatives of *Abies balsamea* and *Picea glauca,* which characterize the transcontinental taiga belt, the term montana taiga has been applied to subalpine forests of the Rockies. Climatic similarity, i.e., heat budgets marginal for tree development, is another point of similarity that is synecologically significant.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Undergrowth plants in this forest likewise bespeak strong affinity with the far North, e.g., *Cornus canadensis, Linnaea borealis, Pyrola* ssp., and *Sorbus scopulina*. In the vicinity of the Canada-United States border *Menziesia ferruginea* and *Xerophyllum tenax* usually dominate over all other undergrowth species. Elsewhere a widespread type has the dwarf *Vaccinium scoparium* as the chief ground cover.

Following fire or logging the first generation forests are typically composed of *Pinus contorta, P. albicaulis, P. monticola,* and *Larix occidentalis* in varying proportions. *Abies lasiocarpa* and *Picea engelmannii* sometimes invade simultaneously but usually they are late-comers. Nearly everywhere the *Abies* slowly increases at the expense of all others, ultimately dominating the climax, except in the few localities where *Tsuga mertensiana* occurs. There the *Tsuga* proves the best competitor. In the krummholz at upper timberline, where the severe climate keeps the tree cover so open that differences in shade-tolerance are not critical, *Abies lasiocarpa* and *Pinus albicaulis* or *P. flevilis* are the main species.

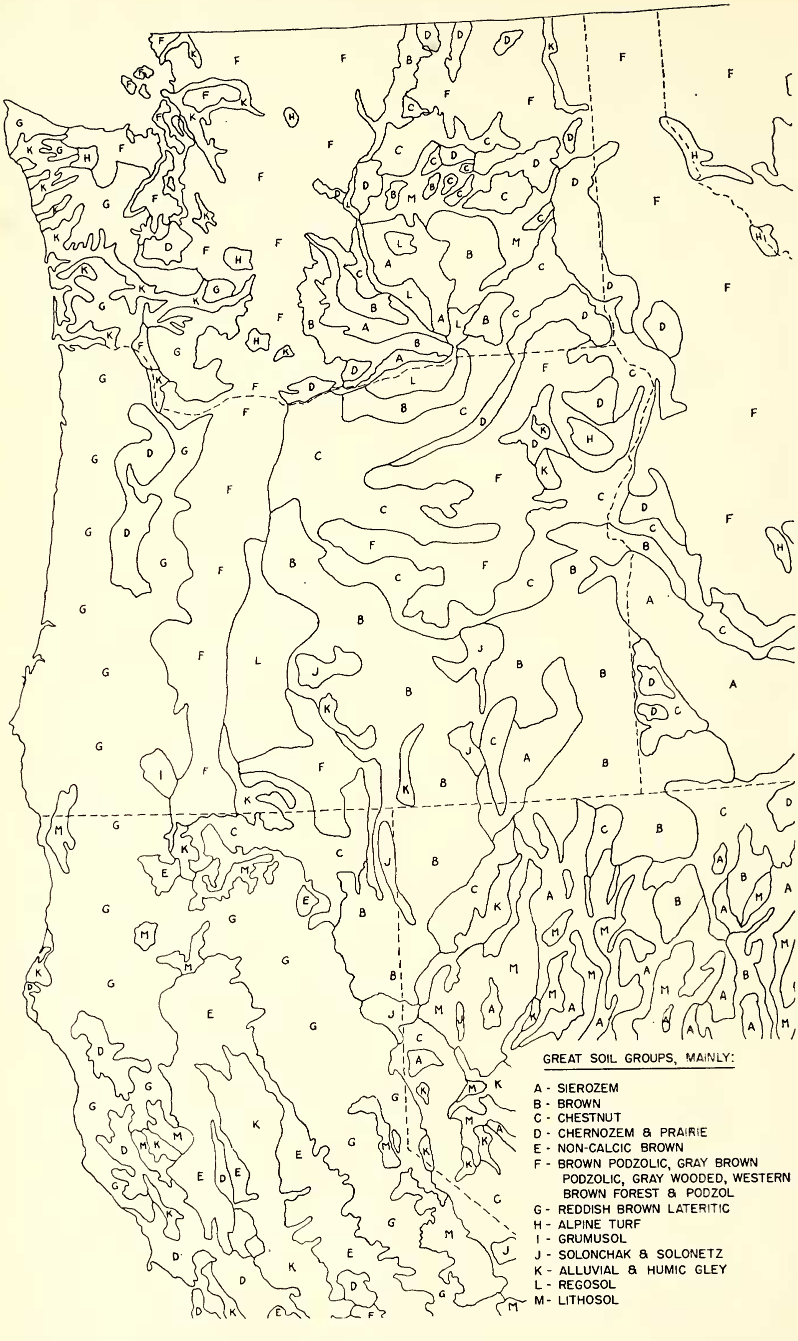
Subalpine forests of the Cascade crest and the few high mountains still closer to the ocean might be bracketed under the term montane taiga only by virtue of their heat budget, since floristic affinities with the transcontinental taiga are essentially nil. Although *Abies lasiocarpa* makes a limited penetration into the strongly oceanic climates, reaching even to the Olympic Mountains, *Picea engelmannii* does not follow it, and instead the major climax dominants there are *Abies amabilis, A. magnifica, Tsuga mertensiana, and Chamaecyparis nootkatensis*. Beneath these trees the common plants include *Menziesia ferruginea, Rhododendron albiflorum, Xerophyllum tenax, Vaccinium ovalifolium, V. membranaceum, Pachistima myrsinites,* and *Pyrola* spp.

Conspicuous trees in the initial regeneration that follows deforestation are *Pseudotsuga menziesii, Larix occidentalis, Abies procera, A. lasiocarpa, Pinus contorta, P. monticola,* and *P. albicaulis*. The last- mentioned becomes especially prominent with *Tsuga mertensiana* in the krummholz at upper timberline.

Montane and Lowland Forests Characteristic of Wet Oceanic Climates

In the region about Seattle natural forest succession usually trends toward the dominance of *Tsuga heterophylla* on well-drained mineral soil. *Acer circinata* and *Cornus nuttallii* are common understory trees. Beneath these trees the two most significant dominants, both evergreen, are *Polystichum munitum* on relatively moist sites or *Gaultheria shallon* on soils having a slight tendency toward dryness. Other common species, most conspicuous under intermediate moisture conditions, are *Berberis nervosa, Clintonia uniflora, Cornus canadensis, Phegopteris dryopteris, Ribes sanguineum,* and *Rubus spectabilis*.

FIG. 2. Mean annual precipitation in inches. Areas with more than 2,540 mm and less than 254 mm have been shaded for emphasis (after Kincer, 1922).


GREAT SOIL GROUPS, MAINLY:
A - SIEROZEM
B - BROWN
C - CHESTNUT
D - CHERNOZEM & PRAIRIE
E - NON-CALCIC BROWN
F - BROWN PODZOLIC, GRAY BROWN PODZOLIC, GRAY WOODED, WESTERN BROWN FOREST & PODZOL
G - REDDISH BROWN LATERITIC
H - ALPINE TURF
I - GRUMUSOL
J - SOLONCHAK & SOLONETZ
K - ALLUVIAL & HUMIC GLEY
L - REGOSOL
M - LITHOSOL

In somewhat swampy situtions *Thuja plicata* maintains dominance indefinitely, and the conspicuous undergrowth plants include *Oplopanax horridum, Athyrium filix-foemina,* and *Lysichiton, americanum.* In valleys too dry for *Tsuga* or *Thuja, Abies grandis* is the climax dominant.

The vegetation as a whole has a lush aspect, with many of the broad-leaved trees, shrubs, and herbs evergreen, as are nearly all the coniferous trees.

Owing to the high incidence of fires in the past, the uplands are most usually dominated by coastal ecotypes of *Psuedotsuga menziesii,* which is the most valuable forest tree of the region and the mainstay of its important forest industry. Old virgin stands of this tree, already established when white man first arrived but no longer common outside national parks, contained individuals up to 127 m tall, with butt diameters up to 7.6 m. *Alnus rubra* is another seral species that is highly aggressive on disturbed land. This is the largest species in its genus and is extensively used for furniture. On recently cut-over lands *Pteridium aquilinum* or the alien *Cytisus scoparius* commonly determine the physiognomy until the first seral forest gets established. In southwestern Oregon *Ulex europea* plays this role.

On moist but not swampy terraces *Acer macrophyllum* is quite common, this tree being an especially good "host" for *Selaginella oregana* which so copiously festoons its branches on the windward side of the Olympic Mountains (especially in the Hoh and Quinault Valleys). *Populus trichocarpa, Rhamnus purshiana,* and *Fraxinus oregana* are other broad-leaved trees common on stream terraces.

Picea sitchensis is mainly confined to a very narrow strip along the open ocean where it plays a climax role under moderate salt spray influence, but becomes seral to *Tsuga* on sandy soils slightly farther back from the ocean. Other trees that are found only close to the ocean are a salt-tolerant ecotype of *Pinus contorta* that is most common on dunes or bogs, and *Chamaecyparis lawsoniana* which is seral to *Tsuga heterophylla* in the Coast Ranges of southern Oregon. Forest along the coast is frequently interrupted by dunes supporting such characteristic species as *Elymus mollis, Carex macrocephala, Lupinus littoralis, Abronia latifolia, Poa macrantha,* and *Lathyrus littoralis,* or by tidewater marshes in which *Distichlis spicata* and *Salicornia pacifica* are the dominants.

Coniferous forests quite similar to those described as characteristic of uplands and swamps back from the influence of sand and salt spray continue from near sea level up the mountains to the lower limits of the subalpine belt, and from British Columbia to southern Oregon, with a disjunct area reappearing on the seaward slope of the major mountain ranges in northern Idaho, northern Montana and southeastern British

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FIG. 3. Principal soil regions. Only the characteristic zonal soil present in each map unit has been indicated (after Various Authors, 1964).

Columbia ("cool moist forests" in figs. 4 and 5). In this inland extension the most notable differences are (1) the substitution of *Pinus monticola* and *Larix occidentalis* as the prevailing seral trees, and (2) the absence of *Gaultheria shallon* and scarcity of *Polystichum munitum* in the undergrowth. In place of these one finds mainly *Clintonia uniflora, Tiarella unifoliata, Phegopteris dryopteris, Viola orbiculata,* and *Vaccinium membranaceum,* all of which occur in the coastal segment, but are overshadowed there by the more conspicuous *Gaultheria, Polystichum, Berberis nervosa,* etc.

The major climax dominants of upland forests in the interior are segregated, with *Tsuga heterophyla* in the most moist situations. *Thuja plicata* in less moist places (but a seral tree on *Tsuga* sites), and *Abies grandis* on soils tending to be drouthy.

Immediately after a fire destroys forests in this group a rich variety of shrubs invades the landscape, and until a new forest canopy develops, this shrubbery provides an abundance of winter browse for deer and wapiti which abound in the area.

Along the coast a related but evidently distinct forest area is one in which *Sequoia sempervirens* dominates, this area extending as a narrow strip from the southwest extremity of Oregon to a little south of San Francisco Bay (see its delimitation in fig. 4). One living *Sequoia* meassured at 117 m tall is thought to be the tallest tree left standing in North America. Pure stands of this species characterize floodplains but on contiguous hillsides *Lithocarpus densiflora, Abies grandis,* and *Pseudotsuga menziesii* form a lower tree stratum. The most abundant plants of the forest floor include *Oxalis rubra, Polystichum munitum, Berberis nervosa, Gaultheria shallon,* and *Vaccinium* spp. *Thuja* and *Tsuga heterophylla* are sparingly represented in the *Sequoia* area.

The southern and inland limits of the *Sequoia sempervirens* forest are associated with the limits of frequent summer fog which results from warm breezes blowing landward across very cold water along the coast.

Forests Characteristic of Moderately Dry to Dry Climates

Soils of the subalpine forests remain moist throughout summer, except perhaps in the top 20 cm or so, and the same is true of those forests below in which *Tsuga, Thuja* or *Abies grandis* are climax dominants. But in passing from the *Abies grandis* areas into land where the soils regularly dry several to many decimeters deep there is a clear ecologic discontinuity. Here *Pseudotsuga menziesii* (or ecologic equivalents) remains free from competition from more shade-tolerant species and so can persist as a major climax dominant, if not the only one. It is desirable to consider separately three geographic subdivisions of this *Pseudotsuga* belt.

In the Willamette Valley of central Oregon (fig. 4) the Douglas fir forest is distinctive for the abundance of *Quercus garryana,* a low deciduous tree which is usually seral to *Pseudotsuga,* but may form pure climax stands in certain relatively dry sites. Small areas in which the *Quercus* plays much the same role also occur on the gravelly outwash plain in Washington southward of Olympia and Tacoma. The deciduous *Holodiscus discolor* is a characteristic shrub of the Douglas fir forest.

Another distinctive segment of what is here referred to as the *Pseudotsuga* belt occurs in the mountains of south central Oregon, extending from there southward in an inverted V-shaped area (delimited in fig. 4) on both sides of the interior valley of California. In this area *Pseudotsuga* is variously associated with *Libocedrus decurrens* and *Abies concolor*. *Pinus ponderosa, P. jeffreyi, P. lambertiana,* and *Sequoiadendron giganteum* are all seral trees here. The last mentioned is famous for its massive trung, which grows to a diameter of 11 m and a height of 100 m, thus dwarfing the climax trees of shorter stature and life-span that grow around it. *Sequoiadendron* trunks may have more than 3500 xylem layers.

Another distinctive feature of this southern Oregon-California sector of Douglas fir belt is the abundance of evergreen sclerophyllous shrubs in the undergrowth. These increase conspicuously in early stage of re generation cycles following deforestation.

A third subdivision of the Douglas fir belt has more distinctly continental climates, occurring on the east-facing slopes of the Cascades, thence eastward in the foothills across the breadth of the Rockies. Here *Pseudotsuga* is the sole climax dominant on zonal soils, with seral trees including *Pinus ponderosa, P. contorta, Larix occidentalis,* and *Populus tremuloides*. In the undergrowth one of the following usually dominates the physiognomy: *Calamagrostis rubescens, Physocarpus malvaceus, Holodiscus discolor* or *Symphoricarpos albus*. On the east flank of the Cascades, *Pinus contorta* is the only conifer that can form forests on large areas of coarse pumice in what appears to be the equivalent climatic belt.

Progressing down the moisture gradient into areas drier than *Pseudotsuga* can tolerate, one sometimes comes abruptly onto steppe on the basal plain, but elsewhere one or two distinctive forest belts may intervene.

If the Douglas fir belt gives way to another forest belt, the later is typically dominated by *Pinus ponderosa* growing in pure stands. These climax pine stands contain a wide variety of undergrowth types depending on variation in climate, aspect or soil, all of which still allow the pine, and only this pine, to form the tree stratum. Some of the undergrowth plants that are locally conspicuous are *Purshia tridentata, Physocarpus malvaceus, Symphoricarpos albus, Festuca idahoensis, F. scabrella, Agropyron spicatum, Stipa comata,* and *Aristida longiseta*. In certain of these forest types the pine grows slowly and is subject to attack and deformation by the parasitic *Arceuthobium campylopodum*, but elsewhere it grows rapidly and provides one of our most valuable timbers. The best growth of the tree, however, is in higher zones where *Pseudotsuga* and *Abies grandis* are climax.

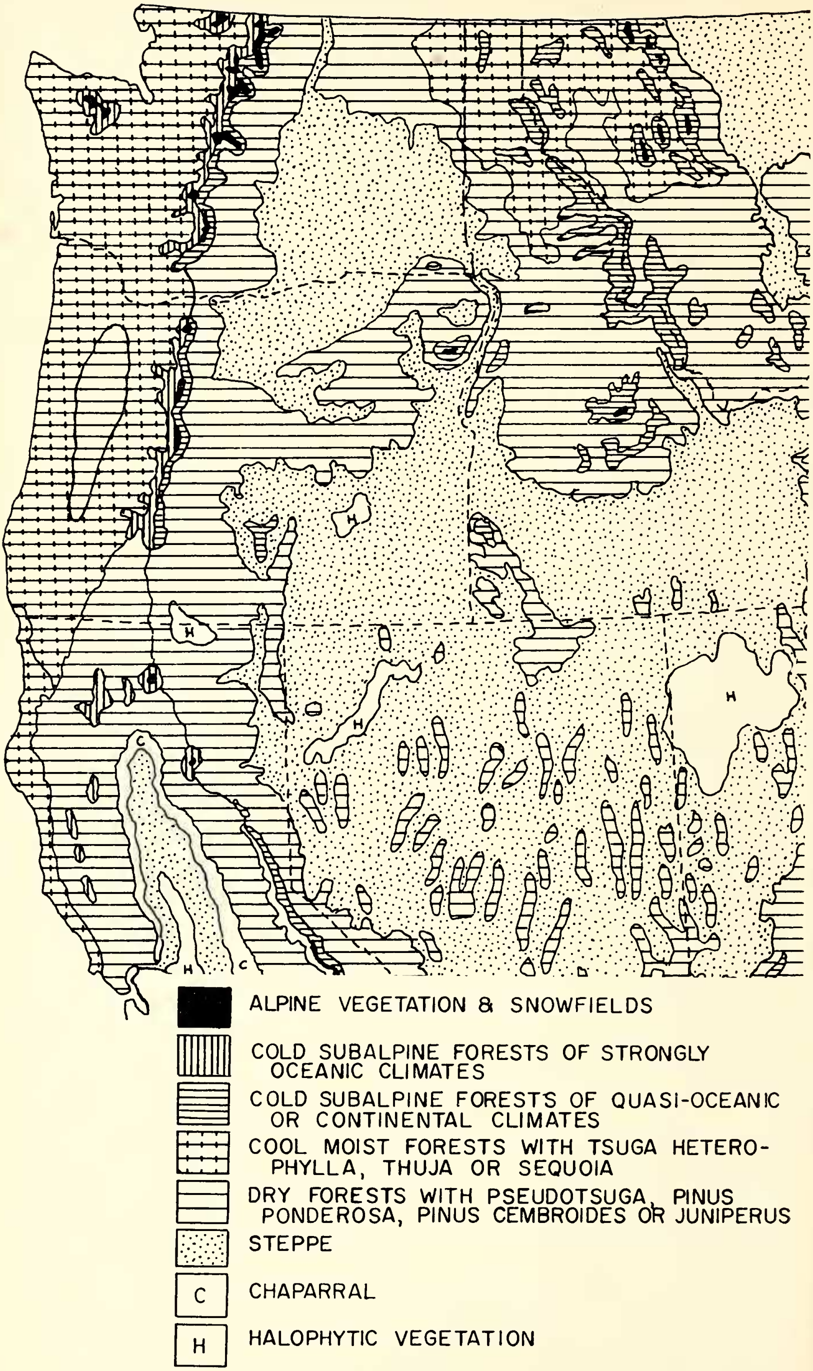

FIG. 4. Vegetation of northwestern U.S.A. (after Shantz & Zon, 1924).

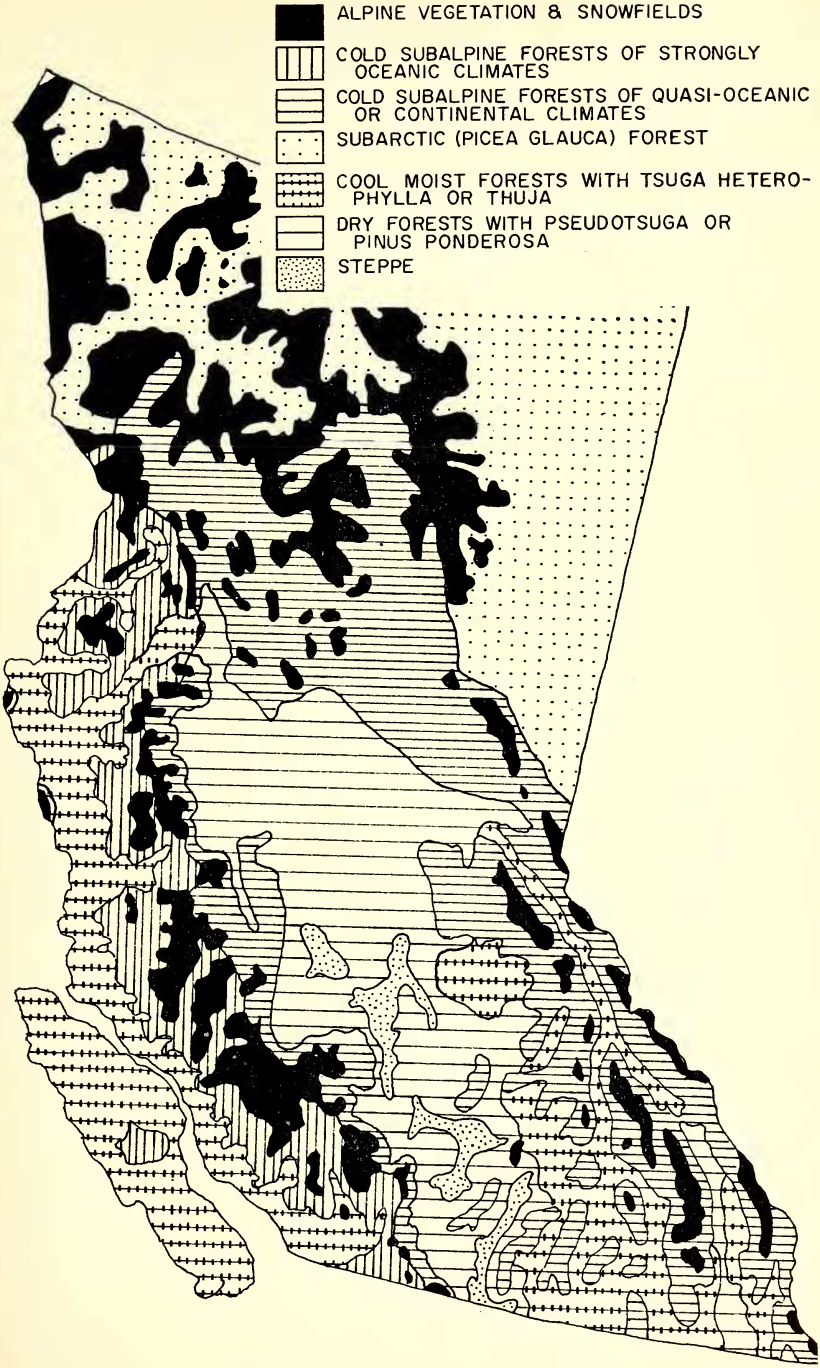

FIG. 5. Vegetation of British Columbia (after Rowe, 1959).

Again as one reaches the lower and drier limit of the *Pinus ponderosa* belt, he may come out onto an unforested basal plain, or he may have one more forest belt to pass through. The last is perhaps better characterized as woodland savanna, for the species of *Juniperus* (*J. scopulorum, J. occidentalis, J. osteospermum*) and *Pinus flexilis* which comprise this type are only a few meters tall and rarely form a closed canopy. This lowest conifer belt is fairly well developed in western Montana, and more locally represented in southern Idaho, and in central Oregon (where the pine does not occur).

On the west side of the Rockies in Washington and British Columbia, groves of *Populus tremuloides* become a conspicuous feature of landscapes in the margin of the steppe, where they are confined to locally moist places.

Chaparral Vegetation

Chaparral vegetation in North America (corresponding to maquis, garigue, fynbos and mallee in other parts of the world) is rather easily divided into three physiognomic categories: scrub (up to 2 m tall), woodland and savanna. All three types are well represented about the margin of the great valley in central California (fig. 4), and the first two extend in fragmentary fashion into southern Oregon.

Chaparral scrub in which *Ceanothus cuneatus, Arctostaphylos viscida, A. canescens, Cercocarpus betuloides, Eriodictyon californicum, Garrya fremontii, Rhamnus californica,* and *Rhus triloba* are major species is locally well represented east of the Coast Ranges in the upper Rogue River Valley of Oregon, with a trace still farther north in the Umpqua River Valley. This scrub occupies a belt marginal to what was originally a small area of steppe, (all too small to show in fig. 4), with *Quercus garryana, Pinus ponderosa* and *Pseudotsuga menziesii* in progressively wetter situations.

Relatively dry ridge summits in southwestern Oregon are in places dominated by *Lithocarpus densiflora* and *Arbutus menziesii* growing as low forest trees with *Rhododendron macrophyllum* forming a tall shrub layer beneath. Stands of this character may be interpreted as the northerly limits of chaparral woodland, which is floristically much more complex southward.

Steppe Vegetation

The low-lying unforested areas between the Cascades and the Rockies are often referred to as "desert" by the local populace. But the few months of intensive summer heat and drouth, combined with the occurrence of cacti, rattlesnakes, scorpions, and tarantulas that perhaps suggest this classification to the layman, do not impress the plant geographer as strongly as does the moderately heavy to heavy stand of perennial grass that grew nearly everywhere before the era of domestic livestock. The term steppe is more appropriate to the botanist.

A good grass cover is possible on practically all soils throughout the arid parts of the Pacific Northwest, for despite the low rainfall, nearly all of it falls in winter when evapotranspiration is feeble and much of the water can percolate deep enough to get below the reach of direct evaporation into the air, thus providing water to sustain a vigorous spurt of vegetative and flowering activity as temperature rises in spring. Summer is mostly a period of aestivation with more plants inactive at this season than in mid-winter. East of the divide of the Rockies most of the rain falls in summer, and the steppe grasses there delay their activity accordingly.

On zonal soils in the steppes of the Pacific Northwest the most characteristic dominants are *Agropyron spictaum, Festuca idahoensis, F. scabrella* (chiefly in British Columbia), and *Poa secunda.* On sandy soils these species are replaced by *Stipa comata, Oryzopsis hymenoides, Agropyron dasystachyum,* and *Sporobolus cryptandrus.*

The driest parts of the intermountain trough from Central British Columbia to central Oregon, together with practically all the intermountain area farther south, originally supported conspicuous but low-growing gray-leaved shrubs that formed a layer well above the grasses, making the term shrub-steppe applicable to this area. Over most of the shrub-steppe *Artemisia tridentata* was the outstanding representative of this shrub layer, with the monotony somewhat relieved locally by other shrubs such as *Chrysothamnus nauseosus, C. viscidiflorus, Tetradymia canescens, Grayia spinosa, Purshia tridentata,* and *Gutierrezia sarothrae.* All these shrubs are deep-rooted, and except for *Grayia* they retain their leaves through the dry summers, with *Artemisia* holding its leaves throughout the year. Herbaceous plants, for the most part the same species as in contiguous steppe lacking shrubs, go into aestivation in midsummer as moisture in the upper meter or more of the profile is used up.

Perennial forbs (*Arnica, Balsamorhiza, Castilleja, Crepis, Geranium, Lupinus, Potentilla,* etc.) are conspicuous in both steppe and shrub-steppe in inverse ratio to the degree of aridity, i.e., they achieve their maximum importance in communities just below lower timberline.

Three cacti occur in the Pacific Northwest—*Opuntia polyacantha* (most widespread), *O. fragilis,* and *Pediocactus simpsonii.*

Over most of the intermountain steppe area the most aggressive plant to assume dominance as grazing eliminates native perennials is the alien *Bromus tectorum.* In the less arid eastern fringe of the steppe it is locally moist enough for *Poa pratensis* to take over this role. In the Great Basin area the noxious alien *Halogeton glomeratus* is relatively more conspicuous in this role.

In eastern Washington and northern Oregon thin stony soils overlying basalt outcroppings are abundant and these support a wide variety of special communities in nearly all of which the tiny perennial *Poa secunda* is the chief grass, with one or more species of dwarf shrubs conspicuous.

Artemisia rigida is the most widespread of these dwarf shrubs, but several species of *Eriogonum* are also common.

Other special soil types in the steppe region support communities in which one of the following is the characteristic dominant: *Eurotia lanata, Artemisia arbuscula, A. nova,* and *Atriplex nuttallii.*

Saline basins in the Great Basin of Utah and Nevada support a rich assortment of halophytic shrubs, forbs, and grasses. The major halophytes here, roughly in order in increasing tolerance of wetness and salinity, are: *Salicornia rubra, Allenrolfea occidentalis, Suaeda depressa, S. intermedia, Distichlis stricta, Atriplex patula, A. argentea, Sporobolus airoides, Puccinellia airoides, Triglochin maritima, Bassia hyssopifolia, Sarcobatus vermiculatus, Atriplex confertifolia, A. nuttallii,* and *Kochia americana.* Northward only a few of this group play the role of major dominants. Here in the north *Distichlis stricta* is ubiquitous. In some places it is associated with *Elymus cinereus,* a coarse caespitose grass growing about 2 m tall, and elsewhere with *Sarcobatus vermiculatus,* a succulent-leaved chenopodiaceous shrub. Marshes in which *Typha latifolia* and *Scirpus* spp. cover large areas are conspicuous in south central Oregon.

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